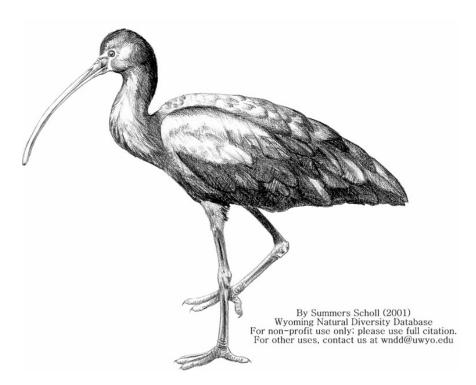
SPECIES ASSESSMENT FOR WHITE-FACED IBIS (PLEGADIS CHIHI) IN WYOMING

prepared by

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Introduction

Plegadis chihi, the White-faced Ibis, is a member of the Ciconiiformes order. They are large, long-legged birds, and they fly with a strong and steady wingbeat (Trost 1989). They are members of the Threskiornithidae family and as such are wading birds. They are gregarious, heronlike birds with long legs and long specialized bills to facilitate feeding in shallow waters (Field Guide to the Birds of North America 1999). They often fly in flocks of 10-50 birds, either in a "V" formation or in long lines, and their only vocalization is a double grunt that sounds like "greh-greh" (Trost 1989).

The White-faced Ibis is an attractive wading bird that is locally common in the western United States, where it breeds. The White-faced Ibis has a long neck, long legs, and a long decurved bill, and inhabits freshwater wetlands and marshes. Like, White Ibises (*Eudocimus albus*), they live and breed exclusively in wetlands, and as a result their habitat is highly dynamic (Frederick and Ogden 1997). This bird has a metallic bronze or dark brown plumage, and in the breeding season, adults have distinctive white feathers along the edge of their faces. The ibis nests in marshes in the western U.S. and winters in large flocks in Mexico, western Louisiana, and eastern Texas. It is a resident in the southern part of its breeding range where it remains year-round. This highly gregarious bird forages and travels in flocks, and nests in colonies. This species eats primarily aquatic insects, crustaceans, and earthworms. It feeds in marshes, as well as flooded hay fields and estuarine wetlands. Breeding occurs in spring (from April – June) and eggs are incubated for a period of 20-26 days. One clutch is laid per year, and usually contains three to four eggs. The young are altricial and both sexes brood and feed the young. Populations decreased in the late 1800's, but today the White-faced Ibis is considered locally common, and populations seem to be

increasing (Ryder and Manry 1994). The conservation of wetland habitat is critical to the continued existence of the White-faced Ibis.

The White-faced Ibis is fairly rare in Wyoming and is known from only eight breeding locations within the state (WYNDD Database). Wyoming does not offer a great deal of suitable nesting habitat for the ibises, but three of the known breeding sites, (Bear River Marshes, Old Eden Reservoir, and Lake Caldwell) have had breeding colonies in most of the last 15-20 years (WYNDD Database).

Natural History

Morphological Description

The White-faced Ibis is a medium sized wading bird, with a long neck, long legs, and a long decurved bill. The bill is distinctive and is 15-18 cm in length (Trost 1989). The White-faced Ibis is dark maroon to brown in coloration, and the bill, legs, and toes are black. Total length is 46-56 cm and weight ranges from 450-525 grams (Ryder and Manry 1994). The total wingspan is 94-99 cm (Trost 1989). In breeding plumage, the head, neck, upper back, wing coverts, and undersides are dark maroon with metallic green and bronze sheen (Figure 1). Wings have a purplish tint to them. Bare facial skin becomes reddish purple, and white feathers appear on the head, separating the forehead from the face. The iris is reddish brown. Nestlings have a black and white banded bill that turns black at fledging, and juveniles have a finely streaked grayish head and lack the white facial markings of adults (Trost 1989).

The Glossy Ibis (*P. falcinellus*) is very similar in overall appearance to the White-faced Ibis, but generally occurs in coastal, eastern North America. A White-faced Ibis in breeding plumage can be distinguished from a Glossy Ibis in breeding plumage, by a red versus brown iris, red versus black facial skin, and red legs versus grayish colored legs (Ryder and Manry 1994). The

Glossy Ibis also lacks the border of white feathers on the head that extend completely around the back of the eye, as in the White-faced Ibis (Ryder and Manry 1994). Adults of both species are often very difficult to distinguish while in the basic (nonbreeding) plumage (Figure 2). Generally, the White-faced Ibis has a red iris (versus brown), and dark facial skin with no border of white feathers (Ryder and Manry 1994). Immatures of both species are often indistinguishable until the White-faced Ibis develops a red iris, usually during its first fall (Ryder and Manry 1994).

Taxonomy and Distribution

Taxonomy

Generally, the White-faced Ibis is considered to be a full species, *Plegadis chihi*, by most taxonomists. The American Ornithologists' Union's checklist (1983), Sibley and Ahlquist (1990), and Hancock et al. (1992) consider the White-faced Ibis to be a species in and of itself. The Glossy Ibis (*Plegadis falcinellus*) is considered by some to be conspecific with the White-faced Ibis. Amadon and Woolfenden (1952), Parkes (1955), and Palmer (1962) consider the White-faced Ibis a subspecies of the Glossy Ibis, and the two species have produced hybrids in captivity (Ryder and Manry 1994). However, in Louisiana, Alabama, and possibly Texas, the two species nest in the same colonies, but apparently do not interbreed (Ryder and Manry 1994). There are no recognized subspecies of the White-faced Ibis (Ryder and Manry 1994).

North American Distribution

The breeding range of the White-faced Ibis (Figure 3) is from northern California, eastern Oregon, southern Idaho, western and southeastern Wyoming, southern Alberta, Montana, eastern North and South Dakota, and just recently northwestern Iowa, south to the Durango and Jalisco states of Mexico (Ryder and Manry 1994). The breeding distribution for Mexico is poorly known. The White-faced Ibis also nests as far south as Tampico Lagoons and Tabasco Lagoons in Mexico,

and there are nesting records from South America as well, mainly southwestern Peru, central Bolivia, Paraguay, and extreme southern Brazil south to central Chile and Argentina.

The winter distribution of the White-faced Ibis is primarily coastal Louisiana and Texas south to the Mexican states of Guerrero, Puebla, and Tabasco, and occasionally to Guatemala and Costa Rica. The White-faced Ibis has also been known to winter locally in southern California and in the lower Colorado River Valley of Arizona (Rosenberg et al. 1991).

Sparse historical records indicate that a wider breeding distribution existed in the late 19th century, than exists today. For instance, a nest at Lake Washington, Florida was reported by Brewster in 1886, and at least two nests were reported from Heron Lake, Minnesota in 1894 and 1895 (Peabody 1896). Although not shown in Figure 3, evidence suggests that in the past two decades the North American population has increased and reclaimed some of its historic breeding range, expanding north to Alberta and east to North and South Dakota, Iowa, and Alabama (Ryder and Manry 1994).

Wyoming Distribution

The White-faced Ibis can normally be found in the southern portion of Wyoming from May through September (Ritter and Cerovski 1990). Within Wyoming there are eight known breeding sites that are distributed across most of the southern half of the state. Within this range (Figure 4), there appear to be two primary zones where breeding occurs from late May through early July (Findholdt 1984). One is in the southwestern corner of the state and is included in the Great Basin localized breeding area and the other is in the southeastern corner of the state in the Laramie plains region. This distribution reflects that most of the suitable habitat and foraging grounds within the state are found only in the southern portion.

The WYNDD database includes 119 White-faced Ibis records, and of these, 79 are considered to be current (less than 15 years old), and 40 are considered historical (Figure 4). There are a total of 41 breeding records for the state, 29 of which are current. There are 78 non-breeding records for the state, 50 of which are current.

The distribution of non-breeding records for the White-faced Ibis in Wyoming extends across much of the southern portion of the state; however, the breeding records seem to be limited to two smaller areas in the southwest and southeast corners of the state. The reasons for this pattern are not known for certain. One consistent feature that all of the breeding records have in common is their proximity to irrigated crops. The ibises have to have foraging grounds near the areas in which they breed. Several of the non-breeding records are also in close proximity to irrigated crops, so this is probably not the sole factor contributing to suitable breeding habitat for ibises in Wyoming. Another factor that may be coming into play is the specific habitat requirements of the ibis. They not only need large wetlands or lakes to breed, but they also require high amounts of emergent vegetation, such as bulrushes, at these wetlands. It seems likely that a combination of factors, such as proximity of foraging grounds and specialized habitat at lakes, play a role in where ibises choose to breed in Wyoming.

Of 119 ibis records for Wyoming, about two thirds of these are less than 15 years old, and one third are more than 15 years old. I believe that the increased number of current records is due to increased survey and search efforts in the last 10 to 15 years (Table 1). Since 1987 the Wyoming Game and Fish Department has been conducting colonial waterbird surveys at various locations around the state. Many of the current WYNDD records are from these surveys. It is likely that ibises have been using certain locations in Wyoming to breed and migrate for the past 20-50 years, but historical documentation of this is lacking.

Habitat Requirements

General habitats where White-faced Ibises can be found regardless of region and season are shallow marshes, ponds, mudflats, and swamps (Ryder and Manry 1994). The White-faced Ibis prefers (almost exclusively) areas with emergent vegetation of some type. The White-faced Ibis inhabits primarily freshwater wetlands and marshes, especially those containing cattail (*Typha* spp.) and bulrush (*Scirpus* spp.) (Ryder and Manry 1994), but it can inhabit estuarine wetlands and coastal areas as well. This bird usually nests in emergent vegetation or low trees and shrubs over shallow water, but it can nest on the ground on small islands as well. Ibises need some degree of isolation by marshes or small islands for both nesting colonies and social night roosts (Trost 1989). At two locations in Utah all nests were in hardstem bulrush (Kaneko 1972) or alkali bulrush (Kotter 1970). A nest's height, above the water or ground, may vary depending upon substrate type and other conditions. In one Utah colony, nests ranged from 99.0-202.2 cm above water that was 61 cm deep (Kaneko 1972).

Foraging Habitat

The White-faced Ibis feeds in flooded hay meadows, agricultural fields, and wetlands (e.g., pond and reservoir margins, mudflats, and marshes) with short, emergent vegetation (Ryder and Manry 1994). Dominant plant species in foraging areas generally are sedges (*Carex* spp.), spikerushes (*Eleocharis* spp.), salt-tolerant grassworts (*Salicornia* spp.), saltgrass (*Distichilus stricta*), and greasewood (*Sarcobatus vermiculatus*) (Ryder and Manry 1994). In Nevada, Colorado, Utah, Idaho, California, and Oregon irrigated crops of alfalfa, barley, and hay are important feeding sites for ibises. In Nevada, White-faced Ibises feed in recently flooded agricultural fields where vegetation is <5 to 90 cm high (Bray 1986), and they show a strong preference for alfalfa fields. Strong preferences were also found for large (>30 ha), level (<5%

slope) fields with clay or clay-loam soils and pools of standing water (Ryder and Manry 1994).

Laubhan and Gammonley (2000) speculated that differences in food abundance, vegetation structure and composition, and behavioral strategies during the breeding season, all influenced the ibis' selection of foraging habitats in the San Luis Valley of Colorado. Along the Louisiana coast, flooded rice fields and livestock pastures over salt marshes are also used as feeding sites (Belknap 1957).

In Wyoming, White-faced Ibises have been noted in marshes, wet meadows, and along vegetated shorelines (Dorn and Dorn 1999). Shallow marshes with emergent vegetation, lakes with vegetated shorelines, and mudflats are preferred habitat, and these areas are often surrounded by sagebrush-grassland or saltbush communities (Merrill et al. 1996). Foraging sites usually consist of shallow wetlands, agricultural fields, and shorelines of ponds and lakes (Ritter and Cerovski 1990).

Summer Habitat (Breeding)

Suitable breeding habitat for the White-faced Ibis includes shallow marshes with "islands" of emergent vegetation, spoil banks of lakes created by dredging, and locally flooded shoals and mangrove swamps (Ryder and Manry 1994). White-faced Ibises generally nest in wetlands on "islands" of emergent vegetation that are either flooded or that extend over the water (Ryder and Manry 1994). However, they can also nest inland in various vegetation types as well. Most inland nesting sites in the Colorado Plateau Province consist of sagebrush (*Artemesia* spp.) and saltbush (*Atriplex* spp.) (Bailey 1978). In the Great Basin most sites consist of hardstem bulrush (*Scirpus acutus*), Olney's bulrush (*S. olneyi*), and alkali bulrush (*S. paludosus*). In Colorado, Baltic rush, sedge, *Carex* spp., and other wetland grasses and forbs are important (Kelli Stone, 2002, pers. comm.), and in California saltcedar (*Tamarix* spp.) and Baltic rush (*Juncus balticus*)

are primarily used (Ivey and Severson 1984). At the Klamath River Basin in Oregon, Taft et al. (2000) observed that White-faced Ibis there rely on early successional emergent plants such as hardstem bulrush for nesting.

In Louisiana and Texas, nests occur mostly in wetlands of outer coastal plains. In Texas, White-faced Ibises were found nesting on bare ground in coastal areas with sea oxeye (*Barrichia frutescens*) (Burger and Miller 1977). In western Louisiana, Belknap (1957) found that freshwater marshes of common reed (*Phragmites communis*), tatora bulrush (*Scirpus californicus*), bulltongue (*Sagittaia angustifolia*), saltmeadow cordgrass (*Spartina patens*), and torpedo panicgrass (*Panicum repens*) are favored habitat of the ibises there, however, Portnoy (1977) found that 55% of >10,000 nests in coastal areas of Louisiana, Mississippi, and Alabama were found in saltwater marshes, compared to 45% in freshwater marshes.

As elsewhere in their range, ibises in Wyoming appear dependent on shallow wetlands with emergent vegetation for nesting. Specifically in Wyoming, White-faced Ibises have been reported nesting in marshes and low trees, or on the ground in bulrushes or reeds (Safran et al. 2000) and in emergent, aquatic vegetation along wetland margins (Ritter and Cerovski 1990). Most nesting sites in Wyoming are dominated by cattail and bulrush species (Ritter and Cerovski 1990), but a White-faced Ibis nest was reported in "decadent greasewood shrubs on an island" at Bamforth Lake in 1988 (Ritter and Cerovksi 1990). This is the only record of this species nesting on an island in Wyoming. Some of the better nesting sites in Wyoming are Old Eden Reservoir, Hutton Lake, and Bear River Marshes.

Spring and Fall Habitat (Migration)

Habitat used by White-faced Ibises during migration is similar to that used during the breeding season, and includes irrigated fields and mud flats along rivers and around lakes and isolated

reservoirs (Taylor et al. 1989). In Oklahoma they have been reported using a variety of habitats from wooded streams to mudflats, and grassy fields bordering playas (Baumgartner and Baumgartner 1992). In California they have been found using sewage aeration ponds (Locatelli and Blankenship 1973), and in Nebraska they have been documented in sandhill ponds and marshes (Ducey 1988).

Some White-faced Ibises do pass through Wyoming on migration routes during the spring and fall. They generally use marshes, small ponds and lakes, and reservoirs to stop at while they are passing through.

Winter Habitat

In Louisiana and Texas, where White-faced Ibises are year-round residents, they use the same coastal wetlands as they do in the summer, as well as inland habitat in flooded rice fields (Remsen et al. 1991). In California they use flooded agricultural fields and natural wetlands (Ryder and Manry 1994). In Mexico they have been observed in central highlands, valleys of high cordillera, and frequenting marshes and irrigated fields (Ryder 1967).

White-faced Ibises do not winter in Wyoming. They generally leave the state around September to fly to wintering grounds in Mexico and the southern U.S.

Territoriality and Area Requirements

Area requirements for individual ibises are not known for certain and there have been no reported studies of what wetland complex size best supports successful, persistent colonies. White-faced Ibises typically defend an area about one meter around the nest (Belknap 1957, Kotter 1970), and they may defend landing and preening perches up to three meters away from their nests (Belknap 1957). Kotter (1970) noted that in Utah there were not any specific spatial relationships required for White-faced Ibis nests. In large colonies, most nests are densely

concentrated at the center and become more isolated at the periphery (Kotter 1970, Kaneko 1972). At a Utah colony in alkali bulrush, distances between ibis nests ranged from 0.5 to 10 meters, averaging about two meters in areas with the highest nest density (Kotter 1970). In Carson Lake, Nevada, a 24 hectare colony in hardstem bulrush averaged 75-150 nests/ hectare (Herron et al. 1987), and in the San Luis Valley in Colorado, ibis nests in hardstem bulrush and cattails averaged 8 meters from the nearest conspecific (n = 43; Schreur 1987). Frederick and Ogden (1997) stated that large White Ibis colonies (> 1,000 pairs) need 800 km2 or more of wetlands to flourish, and proposed that larger wetlands probably tend to sustain colonies for longer periods of time. Little is known about ibis' home ranges outside the breeding season, but during the nesting period in Nevada, most birds foraged three to six km (but up to 18 km) from their breeding colony (Bray 1986). In late summer, prior to the fall migration, breeding adults and recently fledged young have been reported ranging 40-48 km from colonies in Idaho (Trost 1989). No such studies have reported how foraging radius might be affected by breeding colony size or density

Landscape Pattern

Earnst et al. 1998, suggested that the White-faced Ibis would benefit from a landscape mosaic of "well-distributed peripheral wetlands and persistent colony sites." Laubhan and Gammonley (2000) believe that hydrology is the single most important factor influencing ecosystem processes in wetlands, and habitat suitability for the White-faced Ibis. The landscape mosaic must consist of wetlands that have new vegetation growth and that contain suitable water levels (3.5 feet in the San Luis Valley, Colorado) from late April through the end of July (Kelli Stone, 2002, pers. comm.), in order to get the ibises through the breeding season. This year the Monte Vista NWR in Colorado experienced its driest year since 1906, and although some ibises were nesting in late May, they had deserted the site by the middle of June due to several factors, including the lack of new bulrush growth and low water levels (Kelli Stone, 2002, pers. comm.).

Ronald Ryder (2002, pers. comm.) believes that the availability of feeding areas within 10-15 miles of breeding colonies is a very important landscape feature for White-faced Ibises. The importance of foraging areas was demonstrated this summer at the Monte Vista NWR in Colorado, where nesting colonies were deserted in the middle of the breeding season (Kelli Stone, 2002, pers. comm.). Stone believes that the primary reason for abandonment and low reproduction on the refuge was due to the minimal or lack of shallow-water wet meadows where the ibises forage.

Frederick and Ogden (1997) determined the longevity of White Ibis colonies based on an ibis nesting database from Frederick et al. (1996). Their results showed that large colonies of White Ibis (>1,000 pairs) existed for one to 17 years and maintained at least 1,000 pairs during this time. They concluded that there may be a relationship between the size of a wetland and the longevity of ibis colonies. The colonies of greatest longevity, up to 15 years, were associated with relatively large wetlands (100 to 150 km in dimension), and colonies that only existed for 10 years or less were associated with smaller wetlands (less than ten km in dimension) (Frederick and Ogden 1997). Frederick and Ogden (1997) also reported that large, new ibis colonies are generally associated with abnormal abundances of food and exceptional breeding conditions, while abandonment of ibis colonies is associated with degraded breeding conditions and changes in water levels or water management.

Movement and Activity Patterns

Migration

The White-faced Ibis is a highly mobile species, and is considered to be nomadic when not breeding. The northernmost populations undertake large, seasonal north-south migrations. Texas and Louisiana nesters are mainly resident (Ryder and Manry 1994). The White-faced Ibis is well

adapted to finding new nesting areas when regular sites become dry due to droughts (Ryder 1967). Most recoveries of birds banded as nestlings in Utah (205 of 222) have been in Mexico during the non-breeding season (Ryder and Manrey 1994). Some east to west movement is indicated by two recoveries of Utah birds in California, and one recovery of a Nevada bird in California (Ryder and Manry 1994). The Colorado River Valley appears to be an important migration route between the Great Basin nesting areas and the Mexican wintering grounds (Ryder 1967). Most South American populations do not migrate, but South American juveniles do disperse after nesting (Ryder and Manry 1994). Most birds in Utah arrive on nesting grounds sometime in April and leave anytime from late August through early October (Ryder 1967). During migration ibises seek out reservoirs and irrigated fields for resting and feeding (Ryder and Manry 1994). White-faced Ibises arrive in the San Luis Valley in Colorado during April (Schreuer 1987).

Although no Wyoming-specific studies have been done, ibises probably arrive on their Wyoming breeding grounds by late April or early May, and leave by the end of August or early September (WYNDD 2002).

Daily Activity

White-faced Ibises are diurnal, usually feeding during the day and resting at night (Ryder and Manry 1994). The daily time-activity budget of an adult ibis in Florida, during the latter part of nesting, was 13 hours of inactivity (i.e., roosting, resting, and nest attentiveness), 0.75 hours flying, and 10.25 hours foraging (Kushlan 1977). This adult ibis required 203 grams of food per day, or about 21% of its body weight (Kushlan 1977). Kushlan (1977) found that a White-faced Ibis requires 9.2-9.9 x 103 kcal of energy to raise a brood of young. Given the smaller size and shorter nesting cycle of the White-faced Ibis in comparison to larger birds, such as Wood Storks (*Mycteria americana*), the ibis is able to support 11 times the population on only 1.1 times the

energy (Kushlan 1977). This fact may put ibises at an advantage during times of intense resource based selection.

White-faced Ibises do not appear to exhibit any sexually dimorphic movements, such as formation of single-sex post-breeding groups. Very little is known about age-specific activities such as natal dispersal.

Reproduction and Survivorship

Breeding Behavior

White-faced Ibises nest in large colonies that range in size from 30-50 nests in new colonies, up to more than 1,500 nests in older established colonies (Trost 1989). Nest initiation seems to be synchronous within subgroups of ibis, and often in large colonies there are "subcolonies" of 20-30 nests, all of which are at a similar stage (Trost 1989). Once nest initiation has occurred, it is very important that water levels do not drop below 3.5 feet, or else the ibises will desert the colony (Kelli Stone, 2002, pers. comm.).

The mating system of the White-faced Ibis is poorly known, but they are thought to be monogamous. There have never been more than two adult attendants observed at any active nest (Belknap 1957, Kotter 1970). The events leading up to pair formation, and the duration of pair bonds are not known either (Ryder and Manry 1994). In Utah, adults generally begin foraging in pairs one to two weeks before the onset of nesting (Kotter 1970), and in Louisiana pairs arrive at the colony "already mated" (Belknap 1957). Mounting and copulation are preceded by the male stroking and preening the female's dorsal plumage and vibrating his culmen against her rump while she preens her own breast feathers (Ryder and Manry 1994). Copulation occurs at or near the nest site. Extra-pair copulations between adults have not been recorded. Breeding site philopatry is low, as ibises will nest wherever they can find the most suitable habitat (Ryder

1967). Band recoveries suggest that White-faced Ibises regularly use certain breeding and wintering areas, but wander widely depending on water conditions and food availability (Ryder 1967). Both parents care for young. Factors limiting reproduction are nest site availability and food resources. Both must be abundant in order to promote reproduction. No information is available on sex ratios in either the adults or newly hatched birds (Ryder and Manry 1994).

Breeding Phenology

Breeding can be highly synchronous within a large colony, with courting, nest-building, incubation, and fledglings occurring at the same time (Belknap 1957). Seven pairs of White-faced Ibises nesting in the San Luis Valley in Colorado all completed hatching within a 4-day period, indicating that nest initiation was highly synchronous at that site (Schreuer 1987). Ibises may renest if initial breeding attempts fail early in the season, but distinguishing between second nesting efforts and late first nesting efforts is very difficult (Kotter 1970, Bryant 1983). The breeding season in the northern Great Plains (including Wyoming) seems to be up to 1 month later than in the southwestern United States, and this is thought to be the result of cooler early-spring temperatures in the northern areas (Kotter 1970, Steele 1980).

Pair Formation

Pair formation and nest site selection seem to occur from mid April through mid May, shortly after the ibises arrive from their wintering grounds (Ryder and Manry 1994), although some evidence exists that pair formation for ibises nesting in Louisiana may occur prior to arrival at the breeding grounds (Belknap 1957).

Nesting and Egg Laying

Eggs are laid from the second week of April to the last week of June in Utah, and egg laying extended over a period of 41 days in a large colony there (Kotter 1970). Eggs are usually laid in the mornings (Capen 1977) on every other day, and clutches are completed over a period of 5 to 8

days (Kotter 1970, Capen 1977). Mean clutch completion dates have been reported to range from May 14 to May 20 (Kotter 1970, Steele 1980). In Colorado at the Monte Vista NWR, ibises usually have 1-3 eggs by the third week of May and young leave the nest in mid to late July (Kelli Stone, 2002, pers. comm.). Egg-laying dates from June 4 to July 25 in eastern Wyoming and Iowa (Findholdt 1984, Dinsmore and Dinsmore 1986) indicate that breeding occurs several weeks later in the northern Great Plains than in Utah, Nevada, and Colorado. This is probably due to the colder weather in northern areas during the early spring months. In Wyoming, clutches of three to four eggs are probably laid from late April through mid June (WYNDD 2002). Nesting may be delayed if water levels are high or if the vegetation has been damaged by fire or herbivorous mammals (Belknap 1957).

Egg Incubation

Incubation seems to begin soon after the first egg is laid. The incubation period for the first egg in the clutch can be up to seven days longer than for the rest of the eggs in the clutch (Kotter 1970). The average incubation period is 20 days for the terminal egg in the clutch (range 17-21 days, N=40), and up to 26 days for the first egg laid in the clutch (Kotter 1970). Both sexes incubate, but precise sex roles and time budgets are not known.

Hatching

Hatchlings usually emerge within 24 hours of the initial pipping (Kotter 1970). Sequential eggs in the clutch usually hatch one to two days apart, although they can hatch on the same day or up to three days later (Kotter 1970). Young are born semi-altricial (Trost 1989).

Parental Care

Adults brood and shade young continuously from the time they hatch up to two weeks of age (Ryder and Manrey 1994), after which time the young are left unattended for up to three hours at a

time until brooding ceases completely during week three (Belknap 1957, Kotter 1970). Both sexes brood and feed the young (Ryder and Manry 1994).

Fledging/Weaning

Young spend considerable time away from the nest once they are more than 10-12 days old, during which time they engage in preening, loafing, and short flights (Kotter 1970). Young usually fledge at 28+ days (Trost 1989). Fledglings first leave the colony at six to seven weeks of age and are foraging 0.8 km away from the colony by eight weeks of age (Belknap 1957, Kotter 1970).

Natal Dispersal

Young are independent at eight weeks of age (Kotter 1970). There is very little information regarding dispersal. Band recoveries suggest that no yearlings and few second-year birds return to natal areas to breed in the next breeding season (Capen 1977). Adults may leave the breeding colony after the young have fledged, but prebreeding wandering seems more prevalent than postbreeding (Ryder 1967).

Site Fidelity

White-faced Ibises might be described as exhibiting facultative site fidelity, because band recoveries suggest that White-faced Ibises use certain breeding and wintering areas, but that they wander greatly depending on water conditions and the availability of prey (Ryder 1967).

Population Demographics

Fecundity and Survivorship

Age at first reproduction is probably about two years (Capen 1977, Trost 1989), but a quantitative estimate of the average age at first breeding is unknown. Once the White-faced Ibis reaches maturity, it probably breeds annually, unless conditions are not suitable for nesting.

Clutch size ranges from two to five, but is usually three to four eggs (Capen 1977, Trost 1989) and only two young usually fledge due to eggs that don't hatch and mortality of chicks (Trost 1989). Clutch sizes appear to be smaller on average in Texas, perhaps due to undetected loss of weak-shelled, pesticide-laden eggs (King et al. 1980). There is normally one brood per season, unless renesting occurs due to failure of the first attempt. Replacement clutches appear to be less successful than the initial nesting attempts (Capen 1977). In a Carson Lake, Nevada population, the mean clutch size was 3.32 eggs (N=71), 92% of the nests were successful in producing at least one young, and 1.95 young per successful nest (84%) were able to fledge (Henny 1997).

In Utah, the percentage of eggs that successfully hatched ranged from 56% to 66% (66%, n=84 nests; Kotter 1970; 62%, n=53; Kaneko 1972; 56%, n=2,465; Alford 1978). Survival beyond seven to ten days after hatching is difficult to determine because of the mobility of chicks beyond that age. In several studies in Utah, ratios of eggs laid which produced at least one, seven-day-old chick, were 140 of 266 eggs (53%; Kotter 1970), 215 of 478 eggs (45%; Kaneko 1972), and 1,217 of 2,465 eggs (49%; Alford 1978).

Similar studies revealed that in Utah, 53 of 84 nests (63%) produced at least one seven-day-old chick (Kotter 1970); in Nevada, 35 of 42 nests (83%; Henny and Herron 1989). In Colorado, 76 of 111 nests (69%) produced one to four day-old chicks (Schreur 1987).

Exposure of nestlings due to cold, wet weather (Kotter 1970), or high temperatures (Tyler 1933) has been known to cause death in ibis chicks. Heavy rainstorms were reported to kill several nestlings in Utah, either due to drowning or exposure (Kotter 1970). Hatching eggs and small chicks can be killed by fire ants (Solenopsis spp.) on islands off the Texas coast (Burger and Miller 1977). Although numerous predators have been identified (see Community Ecology), predation rates have rarely been documented. Kotter (1970) reported a 28% destruction rate of

White-faced Ibis eggs by Franklin's Gulls (Larus pipixcan) breeding in the same colony in Utah. Mammalian predators seem to cause greater mortalities when water levels are low (Kotter 1970, Capen 1977, Ryder et al. 1979). Steele (1980) determined that large colonies suffer higher predation rates than smaller ones, possibly because they are more conspicuous.

Annual reproductive success of White-faced Ibises in Utah was noted as 1.67, 7-day-old chicks per clutch (n=84; Kotter 1970), 1.42 per clutch (n=151; Kaneko 1972). In Nevada, this figure was 2.54 per successful nest (n=150; Henny and Herron 1989) and in Colorado it was 2.05 ten-day-old chicks per clutch (n=111) and 2.99 per successful nest (n=76; Schreur 1987). Lifetime reproductive success is unknown.

The oldest known White-faced Ibis in the wild was 14 years and 6 months of age (Clapp et al. 1982) and the oldest known ibis in captivity was at least 14 years old (Stott 1948). Based on bird band recoveries from nestlings in Utah, Ryder (1967) found that all birds from this colony had died by the age of 9.

No studies have been done to discern fecundity and survivorship data for White-faced Ibises breeding in Wyoming.

Limiting Factors

Inadequate food sources, lack of suitable nesting habitat, and hydrologic fluctuations of breeding sites are factors that likely limit population growth in this species. Nests may be flooded when water levels rise (Alford 1978) or abandoned after severe thunderstorms (Bryant 1983). Nests are also abandoned when colony sites dry up before the young have fledged (Herron et al. 1987). Habitat destruction and fragmentation of wetlands and marshes also greatly limits population growth in the White-faced Ibis, as it eradicates possible nesting sites.

Metapopulation Dynamics

Given the patchy distribution of White-faced Ibis breeding colonies and the relative mobility of individuals, it is possible that a metapopulation structure exists within the greater North American population, especially in the northwest United States where colonies are particularly disjunct. Moreover, the documented tendency of ibises to abandon unfavorable breeding sites and disperse to suitable areas (Ryder 1967), suggests that geographically proximate colonies could readily experience extinction events followed by recolonization when conditions become more suitable. However, we are aware of no studies investigating the possible metapopulation dynamics of White-faced Ibis colonies, so there is no information on what geographic or temporal parameters might define such a system. There is currently no information to indicate that there are discrete sub-populations that fluctuate separately from others. Estimates defining separation distances that might prevent movement between sub-populations or estimates of how long recolonization might take once suitable conditions are re-established are also lacking.

Genetic Concerns

We are aware of no studies investigating the genetic differentiation of White-faced Ibis colonies or regional populations. Given the broad range of ibises and their lack of natal site fidelity, we would expect genetic mixing to occur such that local populations do not face genetic bottlenecks. The genetic differentiation of White-faced and Glossy Ibises is also uncertain. Ryder and Manry (1994) showed that White-faced Ibis and Glossy Ibis can produce hybrids in captivity, but no records of wild hybrids have been reported, and no genetic studies have investigated the genetic divergence of these two groups.

Food Habits

The White-faced Ibis is classified as a carnivore, piscivore, and invertivore. Main foods taken are aquatic and moist-soil insects, crustaceans, and earthworms (Ryder and Manry 1994). White-faced Ibises are primarily tactile foragers, and they forage in very shallow waters, usually 5-25 cm deep (Kushlan and Bildstein 1992). White-faced Ibises are singularly dependent upon fresh water habitats for foraging because young ibises do not have the ability to excrete salt from estuarine or marine prey (Bildstein 1983). Kushlan (1977) found that White-faced Ibises in Florida consumed an average of 21% of their body weight daily in various prey items.

Food items

Major food items eaten by White-faced Ibises include aquatic and moist-soil invertebrates, especially earthworms and larval insects (Orthoptera, Odonata, Hemiptera, Cleoptera, and Diptera), but also leeches and snails (Capen 1977, Bray 1986, Alcorn 1988). The main food source along reservoir edges is midge larvae (Chironomus spp.) that live in the mud (Trost 1989). Data from 209 White-faced Ibis' stomachs in Utah (52 of which were immature birds) showed that prey items, in descending order of abundance in the diet, were insects, earthworms, leeches, snails, spiders, crayfish, and fish (i.e., carp) (Peterson 1953, Kotter 1970). In Louisiana, items such as crayfish, frogs, snails, and bivalves have also been eaten (Belknap 1957).

There are a myriad of prey items the ibis can eat, but they probably cannot shift prey items altogether. If the ibises cannot find suitable foraging sites with adequate amounts of prey items they will move to a new location where adequate prey is available.

No studies have been done investigating food selection for White-faced Ibises in Wyoming.

Foraging Strategy

White-faced Ibises are primarily tactile foragers and forage in very shallow waters, usually 5-25 cm deep (Kushlan and Bildstein 1992). They locate prey beneath the surface of soil or water by tactile probing. Belknap (1957) describes two distinct aquatic feeding methods for the ibis: (1) a "ranging" method where the ibis walks back and forth and probes the water like a "chicken pecking" in order to capture crayfish and insects, and (2) a stationary method in which the ibis stands in place and swings its bill from side to side in order to catch midge larvae. Water seems to be a requirement for a suitable feeding site as they use standing water to wash soil from prey items (Trost 1989, Ryder and Manry 1994). Long legs, neck, and a long decurved bill are used to facilitate foraging in shallow water and moist soils.

White-faced Ibises feed in large flocks (up to approximately 1,000 birds) and show little aggressive interaction in their feeding groups (Ryder and Manry 1994, Trost 1989). They can fly 40-48 km in the early morning and at dusk between nesting colonies and feeding areas (Trost 1989). They leave roosting and nesting marshes in the early morning to feed in flood-irrigated agricultural fields and at edges of receding irrigation reservoirs (Trost 1989). Bancroft et al. (1994) stated that most White-faced Ibis foraging flights are less than 40 km.

No studies have been specifically addressing foraging strategies of White-faced Ibises in Wyoming.

Foraging Variation

There does not seem to be much variation in food habits for White-faced Ibises of different age classes. Adult ibises of both sexes regurgitate food to chicks until they are six to seven weeks old (Ryder and Manry 1994). Adults and juveniles seem to eat the same basic prey items. Juveniles will forage in groups with adults; however, Bildstein (1983) noted that they usually tend to be with

other juveniles. He also noted that it seems juveniles have to forage longer than adults, perhaps because it is more difficult for them to catch prey. There is no variation in the diets of male and female White-faced Ibises. The only differences in seasonal diets of White-faced Ibises would be for those birds that winter in coastal areas where different prey items exist. Data is somewhat lacking for winter diets of the White-faced Ibis, but they have been observed eating a variety of benthic invertebrates from the Chironomidae and Oligochaeta families in California (Safran et al. 2000), and in Mexico they have been seen eating coprophylic beetles (Coleoptera) and their larvae (Blanco and Rodriguez-Estrella 1998).

No studies have been done investigating the differences in foraging between populations within Wyoming or between Wyoming populations and other North American populations.

Community Ecology

Predation

The habitat of the White-faced Ibis allows them some protection from predators. The emergent vegetation acts as a cover and hides the birds and nest. They nest over water in order to avoid predation by land bearing predators (Ryder and Manry 1994). Predation by gulls, including Franklin's (*Larus pipixcan*), California (*Larus californicus*), and Laughing (*Larus atricilla*), on unguarded chicks and eggs can be a problem (Kotter 1970, Capen 1977, King 1978). Black-billed Magpies (*Pica hudsonia*), grackles, Black-crowned Night-Herons (*Nycticorax nycticorax*), gallinules, Great-horned Owls (*Bubo virginianus*), and Common Ravens (*Corvus corax*) have also been known to pose a threat to eggs and small nestlings (Belknap 1957, Capen 1977, Schreur 1987, Stahlecker 1989). Mink and weasels (Mustela spp.), striped (*Mephitis mephitis*) and spotted skunks(*Spilogale putorius*), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*) can raid ibis colonies, eating eggs, killing chicks, and sometimes adults too, especially when water levels are

low (Kotter 1970, Capen 1977, Ryder et al. 1979). Although predation on adults is not a problem, attacks by Peregrine Falcons (Falco perigrinus), Red-tailed Hawks (*Buteo jamaicensis*), and Greathorned Owls on ibis feeding grounds have been documented (Bray 1986, Kelli Stone 2002, pers. comm.). Ibises are also known to be hunted by humans for food, while on wintering grounds in Mexico (Ryder 1967). Depredation by fire ants (Solenopsis spp.) of hatching eggs and small chicks has been documented on islands off the Texas coast (Burger and Miller 1977).

Interspecific interactions

The White-faced Ibis competes with gulls and grackles for food and will defend a nesting territory from them (Ryder and Manry 1994). This species is commonly parasitized by Blackheaded Ducks (*Heteronetta atricapilla*) in South America (Weller 1968), but there are no reports of interspecific parasitism in North America.

Parasites and Disease

Parasites and disease do not seem to pose a population-level problem for the White-faced Ibis. Botulism can be a problem for ibises in Utah, and regularly sickens and kills them (Wetmore 1918, Ryder and Manry 1994). There are no estimates of how this may impact a population and it is unknown if this is a problem elsewhere in the White-faced Ibis' range. Nymphs of a mite, *Neottialges (Pelecanectes) ibisicola*, were found on a White-faced Ibis in Lubbock Co., Texas (Young and Pence 1979). Overall though, they do not seem to be a problem.

Symbiotic and Mutualistic Interactions

Goossen et al. (1995) reported finding several White-faced Ibis' nests in Black-crowned Night-Heron colonies at various lakes in Canada. This phenomenon has also been reported in the literature by Peabody (1896), and Ivey and Severson (1984). The apparent association between these two species is not well known and benefits from this social attraction are unknown, however, the presence of nesting Black-crowned Night-Herons may indicate favorable nesting conditions to

the ibises (Goosen et al. 1995). This association may be costly as Black-crowned Night-Herons have also been reported to prey on the young of White-faced Ibises (Belknap 1957, Capen 1977).

Conservation

Conservation Status

White-faced Ibis in the Great Basin have been designated as being of conservation concern by multiple agencies (see below) on the basis of the limited number of consistent breeding sites and the uncertain status of many populations (Sharp 1985).

Federal Endangered Species Act

The Great Basin population of the White-faced Ibis was designated a "Category 2 Candidate" for listing as a Threatened or Endangered species by the U.S. Fish & Wildlife Service (1987, 1991), on the basis of the limited number of consistent breeding sites available and the fact that little was known about the condition of the population (Sharp 1985). Since the elimination of the Category 2 list, no formal proposal for listing status of this population has been made. Since this population was only a candidate for listing, never fully proposed, there are no restrictions on this population, and agencies do not have to consider this species with regards to Endangered Species Act stipulations in their management plans.

Bureau of Land Management

The Wyoming Bureau of Land Management (BLM) developed their sensitive species list in 2001, at which time the White-faced Ibis was assigned to that list. The BLM developed the list to "ensure that any actions on public lands consider the overall welfare of these sensitive species and do not contribute to their decline." The BLM's sensitive species management will include: determining the distribution and current habitat needs of each species; incorporating sensitive species in land use and activity plans; developing conservation strategies; ensuring that sensitive

species are considered in NEPA analysis; and prioritizing what conservation work is needed (BLM Wyoming 2001).

Forest Service

Region 2 of the U.S. Forest Service includes the White-faced Ibis on its sensitive species list. Sensitive species are defined by the Forest Service as "those animal species identified by the Regional Forester for which population viability is a concern as evidenced by: (a) significant current or predicted downward trends in population numbers or density, and/or (b) significant current or predicted downward trends in habitat capability that would reduce a species' existing distribution" (USDA Forest Service 1994). The Region 2 area in Wyoming includes the Bighorn, Black Hills, Medicine Bow, and Shoshone National forests and the Thunder Basin National Grassland.

State Wildlife Agencies

The Wyoming Game & Fish Department classifies the White-faced Ibis as having a Native Species Status of NSS3. This status was assigned because White-faced Ibis habitat is restricted or vulnerable in the state (with no recent or significant loss), and populations are declining or restricted in numbers (although extirpation is not imminent) (Oakleaf et al. 2002). Although no regulatory authority is attached to NSS rankings, the Wyoming Game and Fish Department recommends that management agencies potentially affecting ibises should consider the above ranking and all available information on the species.

Heritage Ranks and WYNDD's Wyoming Significance Rank

The Wyoming Natural Diversity Database, as part of the nation-wide network of Natural Heritage programs, has a detailed ranking system which includes global, state, breeding and non-breeding status. The White-faced Ibis has been assigned a rank of G5/S1B,SZN by the Wyoming

Natural Diversity Database. The G-rank (global rank) is a 5-level rank that refers to the range-wide security of native North American species. A rank of G1 indicates the highest degree of endangerment and G5 indicates the lowest. A rank of G5 for the White-faced Ibis specifically indicates that it is demonstrably secure in much of its range, although it may be rare in certain areas, especially at the periphery of its range. The SB-rank (state breeding rank) refers to the security of breeding populations of a migratory species within the state of Wyoming. The White-faced Ibis was given a ranking of S1B because it is considered critically imperiled in Wyoming due to its rarity within the state, its specialized breeding habitat, its low nest site availability, its low population size within the state, its specialized foraging habitat, and threats posed to the species (see Biological Conservation Factors below). The SN-rank (state non-breeding rank) refers to the security of populations that reside in the state of Wyoming during the non-breeding seasons. Since White-faced Ibises migrate out of Wyoming during the non-breeding season, they are not of practical conservation concern in Wyoming during that period. They, therefore, get a rank of SZN, indicating that there are zero definable, manageable non-breeding occurrences.

On a three-level categorical scale (low, medium, high) the Wyoming significance rank for the White-faced Ibis is **Medium**. This ranking is based on a decision ranking tree developed by the Wyoming Natural Diversity Database (Keinath and Beauvais 2003a), and it is designed to consider how Wyoming contributes to the range-wide persistence of a species. The White-faced Ibis is considered a native species to Wyoming, and it is a resident because it has been reliably encountered in Wyoming at multiple locations during the last 10 years. However, the Wyoming distribution encompasses a relatively low percentage of the White-faced Ibis' continental range and is disjunct from other portions the range. Finally, the Wyoming population of the ibis is probably less secure than other populations elsewhere within the species' range, due to limited habitat within the state and the low number of breeders.

Biological Conservation Issues

Abundance

Quantitative estimates of rangewide abundance are not available, due to a lack of consistent census data. The White-faced Ibis is probably fairly common within most of its range, although Breeding Bird Survey data from 1985-1991 indicate that the local abundance varies greatly (Ryder and Manry 1994). The highest abundances (approximately 50 birds per route per year) are in southern Oregon, south-eastern Idaho, central Utah, and along the southern coasts of Texas and Louisiana (Ryder and Manry 1994). Shuford et al. (1996) determined that from 1994-1995 there were approximately 28,000 White-faced Ibises wintering in the Sacramento, San Joaquin, and Colorado River Valleys in California.

Quantitative estimates of abundance within Wyoming are also lacking. In 1997 the Wyoming Game and Fish Department classified the White-faced Ibis as an "uncommon summer resident with relatively few suitable nesting sites and with very low numbers overall" (Oakleaf et al. 1997). These birds winter in the south and only come to Wyoming during the summer months. There are only eight confirmed breeding sites in Wyoming for the White-faced Ibis, and these are not always used every year depending upon habitat conditions at the site (Table 1; Figure 5). Although official population counts in Wyoming have not been done, it is unlikely that there are more than 1,000 individuals in the state in any given breeding season. Numbers of breeding individuals are likewise fairly low. Based on this information, WYNDD categorizes the abundance of White-faced Ibises within Wyoming as very rare (Abundance Rank = A; Keinath and Beauvais 2003b).

Trends

Abundance Trends

In the 1960's and 1970's, nesting populations in North America decreased sharply due to pesticide contamination and loss of habitat (Ryder 1967). However, White-faced Ibis populations

have expanded in the last two decades, in part due to improved nesting habitat management, increased planting of alfalfa crops where birds forage, the banning of DDT in 1970, and improved breeding success at major nesting centers (Ryder and Manry 1994). Since 1970, nesting populations in Idaho (Taylor et al. 1989), Oregon (Ivey et al. 1988), and Nevada (Henny and Herron 1989), have increased dramatically (Figure 6). Modest gains in population were also observed in California (Ryder 1967, Sharp 1985) and in the San Luis Valley of Colorado, where populations have been "booming" in recent years (Ronald Ryder, 2002, pers. comm.). However, the Texas coastal breeding population declined from 6,500 pairs in 1981 to 2,300 pairs in 1990 (M. Lange pers. comm. *in* Ryder and Manry 1994), and the Louisiana coastal population has also declined from 12,495 to 6,225 breeding adults from 1976 to 1990 (Portnoy 1977).

Breeding Bird Survey (BBS) data (Sauer et al. 2001) from 1966-1996 supports the theory that White-faced Ibis populations throughout most of their range have increased, but it indicates that the population in the San Luis River Valley, Colorado, has declined slightly (Figure 6). The Breeding Bird Survey Data also indicates that populations in coastal Texas and Louisiana have increased from 1966-1996, but this contradicts the data from Ryder and Manry (1994) in the above paragraph and may reflect certain constraints of the BBS methodology.

In the western U.S., breeding populations fluctuate markedly in size at the major breeding centers from year to year (Ryder 1967, Steele 1984), and similarly, birds may shift between Texas and Louisiana (King et al. 1980). There have been population increases in Idaho in recent years, but at the same time large colonies in eastern California and the Salt Lake area have been abandoned (Trost 1989). The number of breeding pairs of ibises in Oregon has increased from 600 in 1980, to 2,595 in 1987, and this increase coincided with above average precipitation and record high water levels at many Oregon lakes (Ivey et al. 1988). The population increase in

Oregon, however, is thought to be partially due to the displacement of ibises from nesting areas in marshes of the Great Salt Lake of Utah. These marshes were flooded from 1982-1985 and nesting populations there decreased by as much as 80% during that time (Ivey et al. 1988). It is very difficult to assess the population trends of this species given their nomadic nature, demonstrated in some of the contradicting information presented above.

No systematic study has been conducted, yet since the 1970's, Wyoming has appeared to experience some modest gains in White-faced Ibis populations throughout the state (Ritter and Cerovski 1990). It is difficult to know the exact numbers in a given year, as selected populations have been inconsistently monitored since 1984 (Findholt and Berner 1988) and abundance at localities seems to fluctuate. In addition, some breeding sites are not used every year due to poor habitat conditions or switching from one breeding site to another. Therefore, WYNDD categorizes the abundance trends of White-faced Ibises within Wyoming as uncertain (Trends Abundance Rank = U; Keinath and Beauvais 2003b), due inconsistent monitoring and the general mobility of the species.

Population Extent and Connectivity Trends

The breeding range of the White-faced Ibis has also experienced recent expansions. The first state nesting records for Montana, North and South Dakota, and Iowa were all confirmed in the 1970's and 1980's, as the breeding range expanded into the northern Great Plains (Ryder and Manry 1994). The breeding range also expanded eastward in the late 1970's, through coastal Louisiana to south-western Alabama, widening the zone of overlap with the Glossy Ibis (Duncan and Johnson 1977).

In Wyoming the White-faced Ibis has been observed in 28 of 28 latilong blocks, and there are 8 authenticated breeding colonies in the state that show intermittent use (Table 1; Figure 5) (Trost

1989). Wyoming Game and Fish Department surveys have shown that 4 sites in Wyoming have had fairly consistent use over the last five years. Since 1995 Aurora Lake has had two to six pairs of nesting adults, Hutton/Rush Lakes has had 7-27 pairs of nesting adults, and Old Eden Reservoir has had 1-30 pairs of nesting adults (Table 1). The fourth site that exhibits consistent use is the Bear River Marshes in Lincoln county. This site has exceptionally more use by White-faced Ibises than other sites in Wyoming, and appears to be used on a consistent basis (Figure 5E). The close proximity of the Bear River Marshes to large ibis colonies in Idaho allows ibises to forage between the colonies. Therefore, at any given time there can be hundreds of migrant and foraging ibises at the Bear River Marshes. However, the number of ibises that actually breed at this location is unknown, as often only the number of adults present is counted during surveys. The presence of adults does not necessarily indicate breeding. To confirm breeding status nest counts are necessary, but this is difficult as ibis are very susceptible to human disturbance while nesting. The ibis is only found peripherally in the Greater Yellowstone Ecosystem, but because of their mobility and habit of shifting breeding colonies if conditions are poor, they may be observed almost anywhere within the state where habitat is appropriate (Trost 1989).

It is difficult to say if new colonies have been established in the state recently, due to a lack of monitoring. Aurora Lake may be a new nesting site, but it has only been surveyed since 1990. Ibises were first documented nesting at Aurora Lake in 1996, and have been there every year since, although in very small numbers. The breeding areas in the state seem to encompass the southwest and southeast corners. The southwest corner of Wyoming is close to ibis colonies in other states, such as Idaho and Utah, however, the southeast corner is somewhat isolated from other ibis colonies, both in Wyoming and in other states. The southeast corner, though, appears to have some of the best ibis habitat in the state, as four of the eight known breeding locations in Wyoming occur in the Laramie Plains region. Ibises are strong fliers and can travel large

distances with ease, so connectivity to other breeding colonies may not be crucial. However, connectivity to foraging grounds is an important requirement for ibises.

Trends in Available Habitat

Habitat trends are also difficult to assess due to fluctuations in available habitat relative to precipitation levels. Diversion of natural water supplies from existing wetlands to irrigation projects has led to temporary, or sometimes permanent, abandonment of traditional colony sites (Weller et al. 1958, Ryder et al. 1979). In the Great Basin, loss of wetland habitat has occurred, but it may be partly offset by development of irrigated farmland, upon which the ibises forage extensively (Capen 1977). The effects of wetland destruction on ibis populations in Mexico are unknown, but are cause for concern (Sharp 1985). In Utah and Nevada, some breeding sites have been severely damaged by cattle grazing and trampling (Weller et al. 1958). In some of the federal and state wildlife refuges, burning of emergent vegetation in order to create open water for waterfowl has reduced nesting habitat for the White-faced Ibises (Sharp 1985).

Habitat trends in Wyoming are difficult to assess, due to a lack of information. Considering that many of the breeding sites in Wyoming occur on public lands and receive some form of protection, it is plausible that the habitat at these sites has remained in relatively good condition over the last few years. The trend of habitat availability within Wyoming probably continues to be stable at this time.

Range Context

Most of the White-faced Ibis' range occurs outside of Wyoming. There are only a few local breeding areas within the state, and these do not support large numbers of breeding ibises. The western half of the state, and the southeastern corner are within what one might consider the "core" breeding range of the ibis (Figure 4), but breeding populations are patchily distributed

throughout their range. Ibises breed locally in many areas of the western U. S., and winter in a few areas in southern California, southern Texas and Louisiana, and in central Mexico. Most of the White-faced Ibis' winter range is in Mexico and the southern U.S., and is fairly contiguous. WYNDD categorizes the range context of the White-faced Ibis within Wyoming as low (Range Context Rank = C; Keinath and Beauvais 2003b).

Extrinsic Threats and Reasons for Decline

Anthropogenic Impacts

The greatest human threat to White-faced Ibis populations is habitat degradation and destruction due to agricultural practices. Due to the nomadic nature of the White-faced Ibis, populations would likely decline abruptly and unpredictably as habitat is lost and degraded (Frederick et al. 1996). Diversion of natural water supplies away from existing wetlands to irrigation projects has led to temporary, or sometimes permanent, abandonment of traditional colony sites (Weller et al. 1958, Ryder et al. 1979). In Utah and Nevada, some breeding sites have been severely damaged by cattle grazing and trampling (Weller et al. 1958). In one, atypical case the White-faced Ibis has actually benefited from recent anthropogenic impacts to habitat in Mexico. In the last few years the creation of farms in Mexico has led to more flooded pastures and irrigated croplands that provide valuable feeding areas for the ibises (Blanco and Rodriguez-Estrella 1998).

Pesticide use is one of the major threats to White-faced Ibis populations. DDT-DDE contamination causes eggshell thinning, leading to cracking, denting, or crushing of eggs during incubation. This in turn results in lower hatching success and reduced reproductive output (Capen 1977, Steele 1980). At Carson Lake, Nevada, DDE contamination supposedly reduced the potential fledgling production by at least 20% in 1985 and 1986 (Henny and Herron 1989).

Although DDT was banned in the United States in 1972, DDE concentrations have remained high

in White-faced Ibis populations nesting in the Great Basin region, probably due to DDT use on the wintering grounds in Mexico (Capen 1977, Henny et al. 1985).

Human disturbance of breeding colonies may cause partial or total desertion of nests, especially during nest-site selection, nest-building, and incubation (Ryder and Manry 1994). Biologists working in active colonies must be very careful to avoid disturbing these sites during the sensitive nesting stages.

Hunting of White-faced Ibises was legal in California, Oregon, Texas, and elsewhere in the U.S. until 1918, at which time it was banned (Bent 1926, Ryder 1967). The current extent of illegal hunting in the U.S. is unknown, but is probably negligible (Ryder and Manry 1994). However, hunting on wintering grounds in Mexico continues to be a problem, despite legal protection (Ryder 1967). The impact of hunting on ibis populations wintering in Mexico is unclear at this time (Ryder and Manry 1994).

Anthropogenic impacts in Wyoming are likely similar to those discussed for the entire range of the White-faced Ibis, with cattle grazing and development in wetland areas being a major concern. Many of the breeding locations in Wyoming occur on federal land that is partially protected, so these areas should be free from some detrimental anthropogenic impacts.

Invasive Species

Invasive species are not considered to be a significant contributing factor to the population status of the White-faced Ibis, rangewide or in Wyoming.

Genetic Factors

We are not aware of any genetic studies that have been done at this time on the White-faced Ibis. Genetic concerns may eventually be an issue on the periphery of their range, but ibis mobility is fairly high, so population isolation is likely not a significant factor at this time.

Stochastic Factors (e.g., weather events)

Stochastic factors, such as weather events, can be a problem for ibis populations. Breeding adults will relocate when drought or floods render traditional colony sites temporarily unusable (Ryder 1967, Steele 1984, Taylor et al. 1989). Within the major breeding areas, the Great Salt Lake, Harney Basin, and Lahonton Valley, colony sites change from year to year depending on local water conditions and precipitation levels (Capen 1977, Steele 1984). Nesting sites can dry out and become desiccated in dry years, or they can flood in wet years to the point that they are no longer usable. These stochastic factors can result in loss of nesting habitat, and this can curtail reproduction (Kingery 1976). Droughts can make ibis eggs and young more susceptible to predation. Severe droughts can harm emergent vegetation and it may require several years to regenerate before it can be used by ibises for nesting (Ryder 1967, Herron et al. 1981). Freezing temperatures during early spring can destroy the vegetation that the ibises nest in (Frederick and Ogden 1997), and hurricanes, thunderstorms, and prolonged heat waves can also disrupt breeding at individual sites (Belknap 1957, Bryant 1983, Kingery 1988).

Natural Predation

Predation on adults is probably negligible, although Peregrine Falcons, Red-tailed Hawks, and possibly other large raptors can attack ibises on feeding grounds (Weller et al. 1958, Bray 1986). Predation on White-faced Ibis eggs and young can be a problem. Eggs and small nestlings are at risk to predation from California, Franklin's, and Laughing Gulls, Black-billed Magpies, grackles, and possibly Black-crowned Night-Herons, gallinules, Great-horned Owls, and Common Ravens (Belknap 1957, Kotter 1970, Capen 1977, King 1978, Schreur 1987). Raccoons, striped and spotted skunks, coyotes, mink (*Mustela vison*), and long-tailed weasels (*Mustela frenata*) are all known or suspected to prey on White-faced Ibises at times (Kotter 1970, Capen 1977, Alford 1978, Kingery 1980).

Intrinsic Vulnerability

Habitat Specificity

White-faced Ibises are vulnerable to shifts in habitat quality, since they are habitat specialists, requiring wetland areas, such as ponds, reservoirs, marshes and shorelines with abundant emergent vegetation for nesting. There is some variation in the type of wetland that the ibises can occupy, (e.g., lakes, marshes, etc.), but they need new vegetation growth each breeding season and appropriate water levels (e.g., 3.5 feet in the San Luis Valley, Colorado) from April through July for nesting. Information on colony dynamics of White-faced Ibises in Oregon has shown that they have the ability to compensate for poor conditions at traditional breeding sites by moving among colonies and rapidly colonizing newly available wetlands (Earnst et al. 1998). However, once adults have initiated nesting, the water levels have to remain at suitable levels or the ibises will abandon the nesting colonies.

Territoriality and Area Requirements

There appear to be no quantitatively defined area requirements that would make the White-faced Ibis intrinsically vulnerable to extirpation. Since the White-faced Ibis is a colonial breeder, it is not particularly territorial. Each ibis typically defends small nesting and perching sites within a colony (e.g., several square meters in area), and there appears to be flexibility in the proximity at which they will tolerate other nests. They typically forage several kilometers from nests and do not appear to defend specific foraging sites, so foraging habitat can be distributed over the landscape within a few kilometers of the breeding colony. However, the potential nesting and foraging area required for productive colonies can be fairly large, although minimal area requirements necessary for successful colony formation and reproduction are not known for certain.

Susceptibility to Disease

White-faced Ibises can host several parasites, none of which cause detrimental, population-level problems. Except for botulism, which regularly sickens and kills ibises in Utah (Wetmore 1918, Ryder and Manry 1994), disease does not seem to be a problem causing declines in White-faced Ibis populations either.

Dispersal Capability and Site Fidelity

Despite a lack of quantitative data, it appears that White-faced Ibises can readily disperse and have relatively low site fidelity. Very little information is known about dispersal of White-faced Ibises from breeding sites or colonies, but prebreeding wandering seems to be more prevalent than postbreeding wandering (Ryder 1967). Band recoveries suggest that no yearlings, and only very few second-year birds, return to their natal sites (Capen 1977). Band recoveries also suggest that White-faced Ibises use certain breeding and wintering areas, but they wander greatly depending on water conditions and food availability (Ryder 1967).

Reproductive Capacity

The reproductive capacity of the White-faced Ibis is fairly high (Henny 1997). Age at first reproduction is unknown, but thought to be two years of age (Capen 1977). Once the ibises reach maturity, they will breed annually and have one brood of two to five eggs per year (commonly three to four), as long as conditions are suitable (Ryder and Manry 1994). Usually only two of the young will survive to fledge (Trost 1989).

Sensitivity to Disturbance

White-faced Ibises are very sensitive to human disturbances within their breeding colonies, and this can cause partial or total nest desertion (Ryder and Manry 1994). They are also sensitive to prolonged disturbances, such as drought. After a severe drought it may take emergent vegetation several years to regenerate before it can be used by nesting ibises again (Ryder 1967).

Protected Areas

Range-wide, there has been no official assessment of the actual proportion of White-faced Ibis populations that occur on protected land, where "protected" refers to land that is free from multiple uses that can significantly alter critical habitat for ibises (e.g., wildlife refuges, national parks, wilderness areas). However, White-faced Ibis colonies have been reported at wildlife refuges in Oregon (Malheur NWR, Upper and Lower Klamath NWR), Nevada (Stillwater NWR, Lahontan NWR), and Colorado (Alamosa/Monte Vista NWR).

In Wyoming, much of the White-faced Ibis' range encompasses private land, and very little is known about breeding colonies on private land. Of the eight officially documented breeding sites on public lands in Wyoming (not all of which are used by ibis on a regular basis), three are on National Wildlife Refuges (Bear River Marshes on the Cokeville Meadows NWR, and Hutton and Bamforth Lakes NWR), two occur on multiple-use BLM lands (Old Eden Reservoir and Aurora Lake), one is on multiple-use state land (Bucklin Reservoir), and one (Gellat Lake) is on a Game and Fish Department Wildlife Habitat Management Area.

Population Viability Analyses (PVAs)

The authors are not aware of any formal population viability analyses studies that have been conducted for the White-faced Ibis.

Conservation Action

Existing or Future Conservation Plans

The authors are not aware of any formal habitat management plans or regulations for the White-faced Ibis, however there are some national and regional programs for colonial waterbirds that are in the initial stages. At the national level, the USGS through its Patuxent Wildlife Research Center in Laurel, Maryland, is developing a comprehensive monitoring program for

colonial waterbirds (Steinkamp 2002). One aspect of this monitoring effort will be a centralized database that is incorporated into the National Bird Population Data Center. "This center will integrate information on status, trends, and biogeography of waterbirds across regions, provinces, and states, and will facilitate a coordinated response to conserve these waterbirds throughout their ranges" (Steinkamp 2002). There is also a regional effort being undertaken by the Portland regional office of the U.S. Fish and Wildlife Service. They are in the process of developing regional management guidelines for the White-faced Ibis, as well as other colonial nesting waterbirds, through the Intermountain West Water Bird Management Plan process (Larry Neel, 2002, pers. comm.). This will result in management guidelines for White-faced Ibis in the Great Basin region, a document currently in the approval process.

Conservation Elements

Inventory and Monitoring

Nomadic species like ibises pose special management and conservation challenges because of the large areas they occupy and their unique population dynamics (Frederick et al. 1996). Colonial nesting waterbirds are difficult to inventory and monitor due to their nomadic nature and because they nest in large, interspecific colonies. To date, methods for surveying ibis populations vary across the U.S., from state to state and within regions. A plan is currently underway by the United States Geological Survey and the Fish and Wildlife Service to develop a standardized survey methodology, including frequency and effort, on a national level (Steinkamp 2002). The resulting data should be housed in an accessible, central database.

Several techniques are currently used to survey colonial waterbirds. These methods include flight-line counts from fixed-wing aircraft or helicopter, ground surveys in which nests are counted, and surveys in which colonies are observed in order to count adults present. In most

cases, the number of individual ibises counted is interpreted as an index of the number of breeding pairs. There are problems with most of the survey methods currently being used. Aerial counts are expensive, and though less invasive, tend to miss small colonies. Ground counts of nests are the most accurate way to obtain the number of breeding pairs in a colony, but they can cause a fairly high level of disturbance to the nesting ibises. Ground counts are more cost effective, but they also take longer to complete. One problem with counting adult ibises without any proof of the presence of nests is the difficulty of discerning breeding from foraging or other non-reproductive behavior.

Erwin and Hoover (2002), recommended several protocols to use when inventorying and monitoring colonial waterbird populations. The total number of breeding pairs at a colony in a given breeding season is the ideal value that should be estimated, however this is not always easy to ascertain. Managers will have to decide which factors are most important to them when conducting these colonial waterbird surveys. Erwin and Hoover (2002) state that "desire for accuracy, may come at the cost of disturbance". Some general recommendations for colonial waterbird inventory and monitoring protocols for mixed heronries of intermediate sized birds are as follows:

- Since cost is a factor for most agencies, they suggest monitoring every two to four years consistently among regions, to ensure that metapopulations are being sampled at the same time.
- In northern areas they recommend monitoring any time from June 1 through June 25 and in southern areas any time from late May to early June.
- For larger colonies (>100 nests), they recommend several people enter the colony to flush birds, while two or more observers remain outside of the colony to estimate the number of birds by species. In this case it may be necessary to divide up the species by observer, especially if there are several species within the colony.

- For smaller colonies (<100 nests), they recommend conducting a nest count, but limiting the survey time to 30 minutes or less.
- If estimating abundance of a variety of water bird species, they recommend estimating Black-crowned Night-Herons and ibises first, since these are generally the first to flush from a colony.
- Erwin and Hoover (2002) warn that because the eggs of so many species are indistinguishable, estimating the exact numbers of nests can be quite difficult. In order to "assign" the nests to different species in a mixed colony, they recommend estimating the number of each species flushing from the colony.
- On average, they estimate that one adult equals one nest for most wader species, including ibises (Erwin and Hoover 2002).

Annual or biannual censusing of breeding colonies of White-faced Ibises is consistent and thorough in Nevada (Henny and Herron 1989), Oregon (Ivey et al. 1988), and Texas (Mullins et al. 1982), but it is sporadic and incomplete in various other states such as Idaho, Wyoming, Louisiana, Utah, and California (Ryder and Manry 1994). The nomadic nature of the White-faced Ibis in conjunction with the dynamic nature of its breeding habitat necessitates that wetland management decisions and population monitoring must be conducted in a regional context (Earnst et al. 1998). "In view of the species' nomadism and its apparent tendency to shift breeding areas from one year to the next, monitoring the conservation status of ibis populations would require coordinated surveys that use standardized techniques and that are repeated across the bird's entire range at regular intervals" (Ryder and Manry 1994). Population surveys and status assessments for Mexico are badly needed (Sharp 1985). The Alamosa/Monte Vista NWR in Colorado has been banding ibises for several years and they also have been conducting flight-line counts over the last 4 years (Kelli Stone, 2002, pers. comm.). In the San Luis Valley, Colorado, communication between biologists and wetland managers is integral in developing a complex-

wide management scheme, rather than focusing on discrete wetland units (Kelli Stone, 2002, pers. comm.). There is a San Luis Valley Waterbird Plan that was written in 1995 and is currently under revision.

In the past the Wyoming Game and Fish Department has not been consistent with their methods and level of monitoring of ibises. The limited numbers of ibises and breeding locations in Wyoming should make monitoring and inventorying in the state easier than it is elsewhere. Every two years, if possible, surveys should be conducted at all of the known breeding locations in the state during early June. Many of the small sites can be surveyed by foot, using nest counts, but larger sites may have to be surveyed using a combination of aerial flight-line counts and ground surveys. Ground surveys can be conducted as long as they are kept short.

Habitat Preservation and Restoration

Continued management of wetlands for White-faced Ibis populations is important for preservation of existing breeding colonies. Competition over water rights with irrigation projects, municipalities, and private hunting clubs poses an ongoing threat to many important colony sites in the Great Basin, including some in protected areas (Ryder and Manry 1994). In the late 1980's, negotiations among water users in the Great Basin improved water supplies to critical breeding areas in Lahontan Valley, Nevada (Sharp 1985) and Harney Basin, Oregon (G. Ivey pers. comm. *in* Ryder and Manry 1994). A good example of habitat preservation during a drought comes from Carson Lake, Nevada, where a limited water allotment was concentrated in a single management unit to accommodate ibis nesting (Herron et al. 1989). Breeding success and total fledgling production at the site were exceptionally high that year, despite the drought conditions (Herron et al. 1989). The U.S. Fish and Wildlife Service is known to employ methods to restore quality

nesting habitats for colonial waterbirds, such as manipulating vegetative structure and water levels to favor waterbirds, and minimizing human disturbances at colonies.

Captive Propagation and Reintroduction

At this time, no efforts have been taken in regards to captive propagation and reintroduction for White-faced Ibis populations. These efforts are probably not warranted at this time given current population status. Habitat preservation is more important at this point in order to sustain populations and promote growth.

Information Needs

Range-wide Needs

Habitat use, feeding ecology, and breeding biology are poorly documented in the Gulf Coast regions and these need to be studied (Ryder and Manry 1994). The breeding range of White-faced Ibises overwintering in central and southern California needs to be determined, as these birds may constitute a resident population that does not migrate south in the winter (Ryder and Manry 1994). A population survey of ibises in their winter ranges needs to be monitored via coordinated and standardized surveys (Shuford et al. 1996), to determine the extent to which impacts on wintering grounds are affecting breeding populations. A great deal of this species' general behavior is not known, and efforts need to be made to ascertain information on communication behaviors, pair formation, pair-bond duration, breeding and natal dispersal, and time budgets (Ryder and Manry 1994). Data on the distribution, population status, and breeding of White-faced Ibis populations in Mexico is greatly needed (Sharp 1985). Monitoring of pesticides and other contaminants needs to be maintained, and the effects of these contaminants on ibis mortality and reproduction should be also studied (Ryder and Manry 1994). We would also suggest the need for quantifying the resources necessary for colony establishment and successful breeding. For example, determining

the thresholds of wetland size, hydrology, and water quality that can support successful colonies would greatly benefit the land manager seeking to maintain colony health or facilitate colony formation.

Wyoming Needs

Wyoming needs include surveys for all areas of suitable habitat within the state in order to know what kind of breeding populations the state can support. Since managers are currently focused on public land, it would be best to expand this to include identification of colonies occurring on private land. Monitoring of existing populations in a statistically valid and repeatable fashion is very important, so trend estimates can be reliably referenced. It would also be valuable to try to identify new breeding locations in the state. This could be accomplished by conducting surveys at locations where ibises have been observed in the past, but not documented to be breeding. Based on WYNDD's records, some specific areas that may be good to search include Fontenelle Reservoir in Lincoln county, Lyman Lake and Cliff Graham Reservoir in Uinta county, and Table Mountain Wildlife Habitat Unit in Goshen county.

Also, Wyoming specific data is lacking for numerous aspects of the White-faced Ibis' behavior, biology, and ecology. Pesticide levels in Wyoming populations should also be checked and monitored.

Tables and Figures

Table 1: White-faced Ibis survey data from 1984-2000. Shaded areas indicate years where populations were actually surveyed. Unless otherwise noted, records are from the Wyoming Game and Fish Department Nongame Program Annual Completion Reports from 1988 – 2001. There are 8 known breeding locations in the state; 7 are listed in the table. The 8th location is a 1998 record from Romney Pond on the National Elk Refuge near Jackson, Wyoming, which is not regularly surveyed for ibis.

	Aurora	Bamforth/	Bear River Marshes	Hutton/Rush	Old Eden	Caldwell	Pilger
	Lake	Carroll Lakes		Lakes	Reservoir	Lake	Lake
1984	Not surveyed	No ibises found ^a	No ibises found ^a	No ibises found ^a	Not surveyed	Not surveyed	Not surveyed
1985	Not surveyed	No ibises found ^b	No ibises found ^b	No ibises found ^b	No ibises found ^b	Not surveyed	Not surveyed
1986	Not surveyed	Not surveyed	33 nests ^b	Not surveyed	14 nests ^b	19 nests ^b	Not surveyed
1987	Not surveyed	1 pair adults exhibited weak nest defense	985 adults and fledglings, no active nests seen	No ibises found	5 nests	5 nests	No ibises found
1988	Not surveyed	20 young, no nest count	Not surveyed	Not surveyed	Not surveyed	Not surveyed	Not surveyed
1989	??	??	??	??	??	??	??
1990	First surveyed; no ibises found	No ibises found	186 ibises; 6 nests	Not surveyed	No ibises found	6 nests	Not surveyed
1991	No ibises found	No ibises found	Not surveyed	Not surveyed	Not surveyed	Not surveyed	Not surveyed
1992	No ibises found	No ibises found	Not surveyed	Not surveyed	Not surveyed	Not surveyed	Not surveyed
1993	No ibises found	No ibises found	Not surveyed	Not surveyed	2 adults with a nest of 3 young	Not surveyed	Not surveyed
1994	No ibises found	No ibises found	74 adults, nesting not confirmed	No ibises found	No ibises found	2 nests with a total of 3 eggs	No ibises found
1995	No ibises found	No ibises found	91 nests	Not surveyed	No ibises found	Adults observed; no nests found	Not surveyed
1996	4 adults 2 nests*	No ibises found	385 nests with 562 young and 737 eggs	22 adults 11 nests*	3 nests with 9 eggs total	11 adults 6 nests*	26 adults 13 nests*
1997	4 adults; 2 nests*	No ibises found	30 adults; No nest count	54 adults; 27 nests*	1 nest with 2 young	No ibises found	No ibises found
1998	4 adults; 2 nests*	No ibises found	210 adults. No nest count	50 adults; 25 nests*	30 adults; 15 nests*	44 adults; 22 nests	No ibises found
1999	5 adults 3 nests*	No ibises found	360 adults Nests not counted	20 adults	60 adults 30 nests*	No ibises found	16 adults
2000	12 adults; 6 nests*	No ibises found	460 adults; 200 nests*	14 adults; 7 nests*	3 adults; 1 nest*	No ibises found	1 adult

^{* -} The number of nests indicated is an estimate based on the number of adults observed and assumed to be breeding.

^{?? -} The 1989-1990 Game & Fish Report is either missing or they did not put one out for this year.

^a – These records are from Findholt 1984.

^b – These records are from Findholt and Berner 1988.

Figure 1: Photo of a White-faced Ibis in breeding plumage at the Alamosa National Wildlife Refuge in Colorado. (Photo by Tom Smylie© 1970)



Figure 2: Photo of a White-faced Ibis in non-breeding plumage. (Photo by George Jameson).



Figure 3: Rangewide distribution map for the White-faced Ibis.

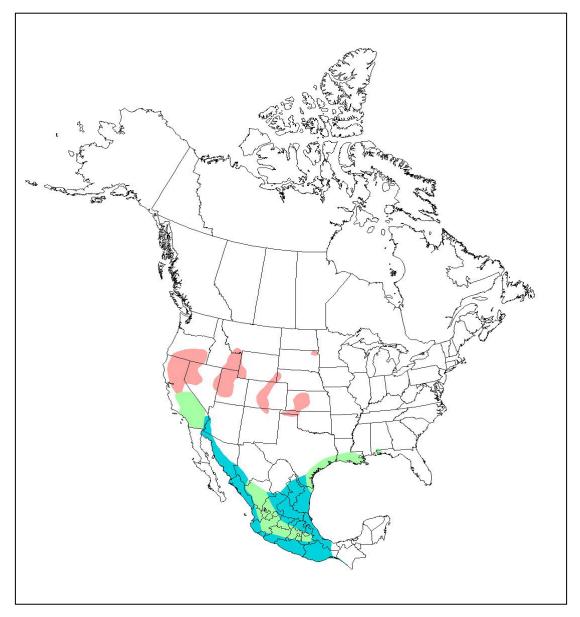
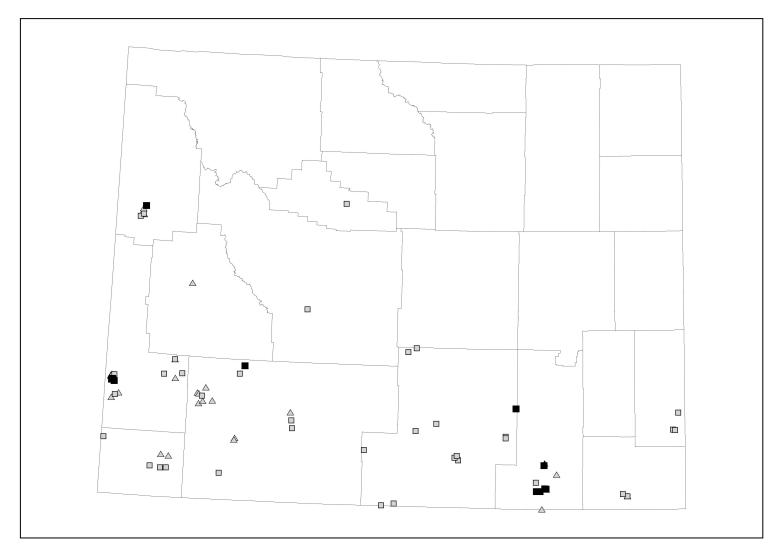




Figure 4: Reported Wyoming White-faced Ibis current breeding occurrences.



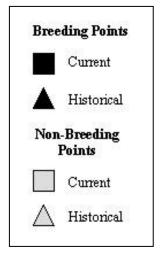
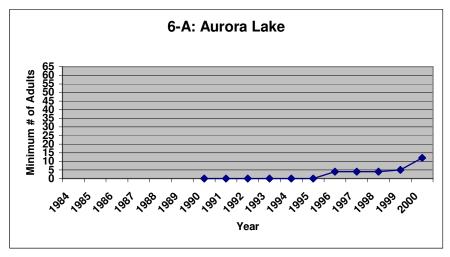
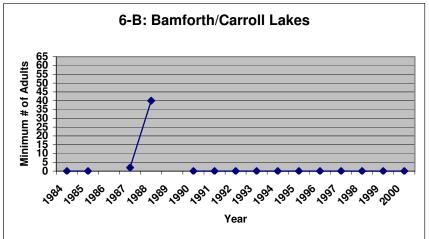
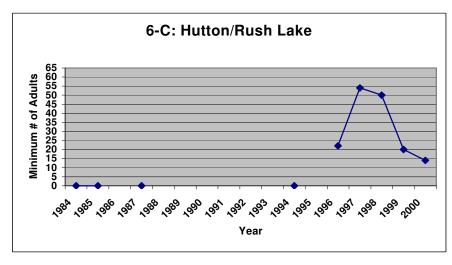


Figure 5: A-G; Trends in numbers of adult ibises at seven known breeding locations in Wyoming (based on # of adults or nests counted) and map. Gaps in the data represent years when surveys were not conducted. Note, the Y Axis for E is different than the others.







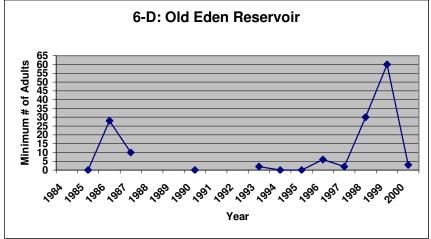
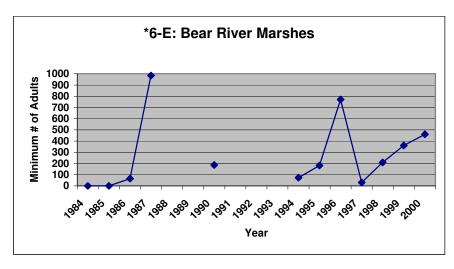
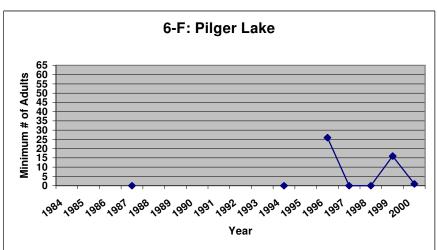


Figure 5 cont.





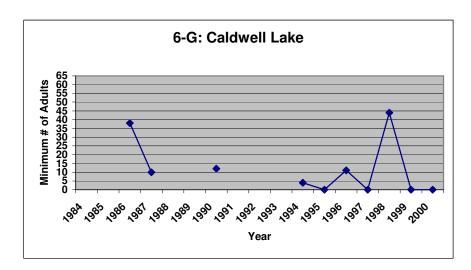
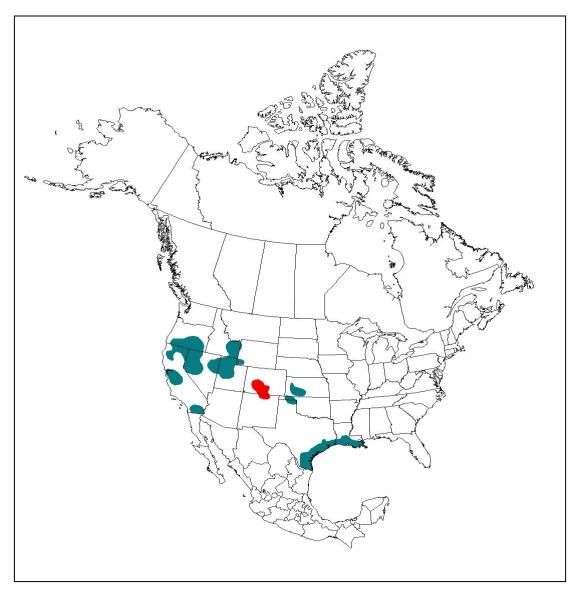
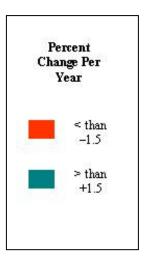


Figure 6: Population trends of the White-faced Ibis in the United States, 1966-1996, based on data from the Breeding Bird Survey (Sauer et al. 2001).





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